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AN ANALYSIS OF THE RELATION BETWEEN THE TEMPERATURE AND THE DURATION OF A BIOLOGICAL PROCESS

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1. Biological processes exhibit variations in rate at different temperatures. The speed of a given activity increases with an increase in the temperature, usually in the form of an exponential function, occasionally in a linear manner. At higher temperatures, however, the rate of increase falls off. The velocity of the process reaches a maximum at a critical temperature, above which the activity declines rapidly or ceases entirely.

Such vital processes are undoubtedly conditioned by chemical and physical reactions. It should therefore be possible to analyze these variations in terms of the changes usually associated with the relation between chemical and physical reactions and the temperatures at which they occur. This has been difficult to accomplish except in the most general terms. The variations at higher temperatures are attributed to the destructive effect of heat on protoplasm, etc., but no really quantitative analysis of such variations is attempted. It has, however, been possible to accomplish this in a study of the photic sensitivity of *Mya arenaria*.

2. The mollusc *Mya* responds to illumination by a rapid retraction of its siphons. Its reaction time is composed of two parts. The first is a sensitization period during which the animal must be exposed to light in order to respond at the end of the usual reaction time. The second is a latent period during which *Mya* may remain in the dark. At the end of this period the organism responds as if it had been exposed to light for the entire reaction time. The composition of the reaction time is strikingly clear, because the sensitization period is very short,—less than 0.10 second at moderate intensities. The latent period, however, is well above 1.0 second at room temperature.

The sensitization period is conditioned by the velocity of a photochemical reaction. The more intense the stimulating light, the shorter is the time necessary to exposé Mya in order to produce a response.

The latent period, however, depends on a reaction, the velocity of which is determined by the amount of substance formed during the exposure to light. The reciprocal of the latent period measures the velocity of its determining reaction. The relation between the velocity and the exposure time is strictly linear for exposures shorter than the sensitization period. Since it is generally true that the velocity of a catalyzed reaction is a linear function of the concentration of catalyst, the latent period is very probably the result of a chemical reaction which is catalyzed by the substance formed during the exposure to light.

This intimate connection between the two phases of the reaction time makes it possible to investigate the relation between the temperature and the latent period, free from the usual 'rate of heating' and 'time factor' difficulties. By bringing the animal to the desired temperature in the dark, errors resulting from the change of the system during the preliminary and subsequent heatings are largely eliminated. This is because the products of the reaction concerned with the latent period occur only as an immediate result of the exposure to light. They can, therefore, be influenced only after such exposure. The changes which then occur are exactly the ones which it is desired to measure.

The results obtained by determining the latent period at different temperatures, at a constant intensity, will be found in detail in a future number of the Journal of General Physiology. They are, in general, similar to the many that have already been published, with the exception that they are amenable to a clear analysis. With this we shall now be concerned.

3. The relation between the velocity constants (K_1 and K_0) of a chemical reaction at different temperatures (T_1 and T_0), is given by Arrhenius in the following equation:

$$\frac{K_1}{K_0} = e^{\frac{\mu}{2}\left(\frac{T_1-T_0}{T_1T_0}\right)}.$$

The temperatures are absolute, e is the Naperian base, and μ is a constant characteristic of a given chemical reaction. Since only the ratio between the velocity constants is required, there may be substituted in their places the reciprocals of the time required to accomplish a given amount of work.

Using the reciprocals of the latent period at different temperatures in this manner, μ shows a constant value of 19,680 from 13° to 21°C. Between these temperatures the latent period, therefore, varies as if it were conditioned by a single chemical reaction. Above 21°, however, the value of μ decreases steadily until at 31° it is 11,210. This regular decline in the value of μ is equivalent to saying that above 21° the latent period becomes longer than it would be if the process as a whole showed a constant value of μ. At higher temperatures, therefore, the operation of a secondary factor becomes evident. The effect of this is to increase the duration of the reaction concerned fundamentally with the latent period.

4. The steady decrease in the value of μ with rising temperature indicates an increasing effect of the second factor. The results of its operation below 21° are probably not measurable. It should be pointed out that 21°C. is the mean water temperature of the hottest month at Woods Hole.

If we conceive the substance formed during the latent period to be thermolabile, and also that a definite quantity of it is required to cause a response of the animal, the presence of this secondary, modifying factor may be quantitatively determined. At higher temperatures the thermolabile substance is rendered inactive in appreciable amounts. Consequently the reaction producing the thermolabile substance must proceed longer in order to make up the amount of it required for a response. The interval of time in which all this occurs is very small at temperatures above 21°,—less than one second. The portion of the reaction isotherm which is involved may therefore be considered a straight line. The amount of thermolabile substance formed will thus be a linear function of the time.

By using the original, constant value of μ ($=19{,}680$), it is possible to calculate the duration of the latent period at higher temperatures, free from the influence of the additional variable. The differences between the calculated time and the observed time serve as a measure of the effect of the second factor. The difference in time divided by the calculated time gives the per cent of the theoretically necessary amount of thermolabile substance which is inactivated at any temperature.

It has been repeatedly shown that the course of inactivation reactions and of spontaneous decompositions agrees well with that of a reaction of the first order. Therefore, from the above results, isotherms may be constructed showing the partial course of the inactivating reaction here concerned, at different temperatures. It is thus possible to find the time required to inactivate a given amount of thermolabile substance at the various temperatures. The reciprocals of the time may now be substituted in the above equation of Arrhenius, and the value of μ determined.

When these steps are followed, the inactivating reaction shows a constant value of $\mu = 66{,}800$. High values for μ, of the same order of magnitude as here given, obtain generally for spontaneous destructions, inactivations, and coagulations. The fact that the value of μ corresponds to those found for similar processes strengthens the force of the reasoning which underlies the analysis here presented.

It is, therefore, permissible to conclude that the duration of the latent period in the photic response of *Mya*, at the temperatures studied, is conditioned by two chemical reactions. The first is the fundamental reaction which determines the nature of the latent period. The second is a reaction which inactivates the principal product of the fundamental reaction, thereby prolonging the latent period at higher temperatures.